THE ACOUSTIC BIOLOGY OF SNAKES

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■ INTRODUCTION

Snakes remain a rather enigmatic group of animals. Recent studies have shown that aspects of the biology of snakes, particularly their behavioral ecology, are more varied and complex than was previously realized (for an excellent discussion see Greene, 1997). Despite this, an overly generalized and stereotypic conception of snakes is still frequently encountered; this is particularly true of the acoustic biology of snakes. Acoustic biology refers to the total influence of sound on the biology - primarily the behavior - of the organism. Although other subdivisions are possible, herein three aspects of acoustic biology will be discussed; hearing, sound production, and the behavioral significance of sound. These three general topics serve to illustrate just how enigmatic snakes remain.

■ HEARING IN SNAKES

The early literature is surprisingly rich in descriptions and experiments intended to address the question of hearing in snakes. The absence of an external tympanic membrane in all snakes, coupled with their presumed behavioral indifference to sound, was generally regarded as strong evidence that snakes are deaf (see Young, 1997a,b). Thanks to several physiological experiments, we now know that not only can snakes hear, but they can hear airborne sounds as well as groundborne vibrations (see Hartline, 1971a,b; Wever, 1978). Unfortunately, few studies have expanded on these early physiological experiments; as such, there are many perplexing questions about both the mechanism and behavioral importance of hearing in snakes. The approximately 20 species of snakes examined by these physiologists showed a rather lirmited acoustic sensitivity, with physiological responses to sounds between 150 - 1,000 Hertz, and a peak sensitivity of around 300 Hertz. While these species had some variation in their acoustic sensitivities, none appeared to have acoustic specializations associated with aspects of their behavioral ecology. It would be interesting to study the variation in acoustic sensitivity within a closely related group of snakes which have different habitat and prey preferences.

While the physiological experiments demonstrated that snakes can hear, the mechanism by which vibrations reach the inner ear remains unknown. There appear to be at least three different pathways for the transmission of vibrations:

1. groundborne vibrations can be transmitted through the lower jaw to the quadrate and then via the stapes to the inner ear (Figure 1);

2. airborne stimuli applied over the quadrate can be transmitted via the stapes to the inner ear (Wever and Vernon, 1960); and,

3. perhaps most interestingly, vibrations (both groundborne and airborne) applied along the snake's body can also produce neural activity in the inner ear.

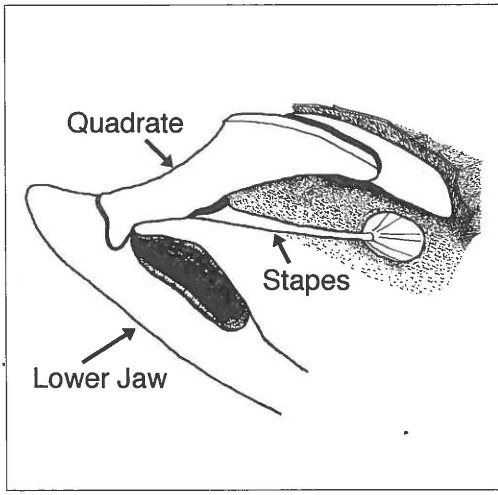

Fig. 1
Diagrammatic view of the lateral surface of a snake's skull. The stapes transmits vibrations to the inner ear (located within the skull); the connections between the stapes, quadrate, and lower jaw appear to enable the snake to respond to both airborne and groundborne vibrations.

This last mode of vibration transmission, termed the somatic system (Hartline and Campbell, 1969), is still poorly understood. Is the vibration stimulating one of the many sense organs located in the snake's skin, or is it being transmitted by the lung or other visceral organs? The degree to which the somatic and auditory systems may respond to different stimuli (such as airborne versus groundborne), the integration of these two systems in the brain, and the extent of interspecific variation between these two systems remains unknown.

■ SOUND PRODUCTION IN SNAKES

Sound production in snakes can not be simply equated to rattling in rattlesnakes and hissing in other species, for there are diverse methods used by snakes to produce sound (Young, 1997a, Gans and Maderson, 1973). Snakes can produce sound through vibration of the tail with or without a specialized rattle, by expulsion of air from the cloaca (Young and Abishahin, 1998), by rubbing body scales together, or by hissing. Although all crotalids appear to rattle in the same way (Young and Brown, 1993, 1995; Cook et al., 1994), snakes hiss in many different ways. The king cobra (*Ophiophagus hannah*) and other species have outpocketings from their trachea which enable them to produce a deep resonating hiss often called a growl (Young, 1991). The larynx of the pine snake, *Pituophis melanoleucus*, includes a

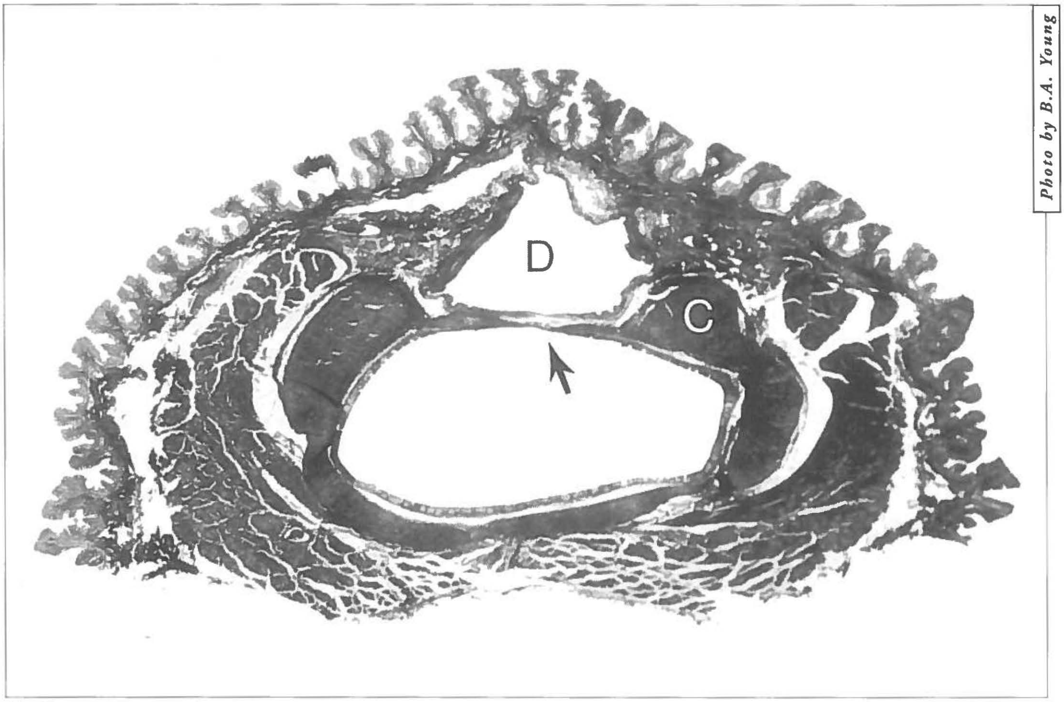

Fig. 2
Micrograph of the larynx of Pituophis melanoleucus showing the vocal cord (arrow) attached to the cricoid cartilage (C) and separating the larynx into the small blind-ending dorsal chamber (D) and the large ventral chamber which leads to the glottal opening.

small vocal cord (Figure 2) which appears to produce the shrill hiss of that species (Young et al., 1995). While many snakes hiss with their mouth open, others, including the hognose snakes (*Heterodon*) hiss through their nose while the mouth is kept closed (Young and Lalor, 1998).

These different mechanisms of sound production are an important part of the acoustic biology of snakes because each mechanism may produce a different sound. The rattle of a rattlesnake, the cloacal pop of a coral snake, the growl of a king cobra, or the hiss of a puff adder are all qualitatively and quantitatively distinct sounds (Figure 3). Even species which produce sound in the same way (i.e., hissing with the mouth open) may produce sounds of different duration, intensity, or frequency range. These different snake sounds all share one feature, they are all acoustically simple. No snake sound has been described which includes either regulated temporal patteming, frequency modulation, or amplitude modulation. The sounds made by snakes appear to be "all or none" acoustic events.

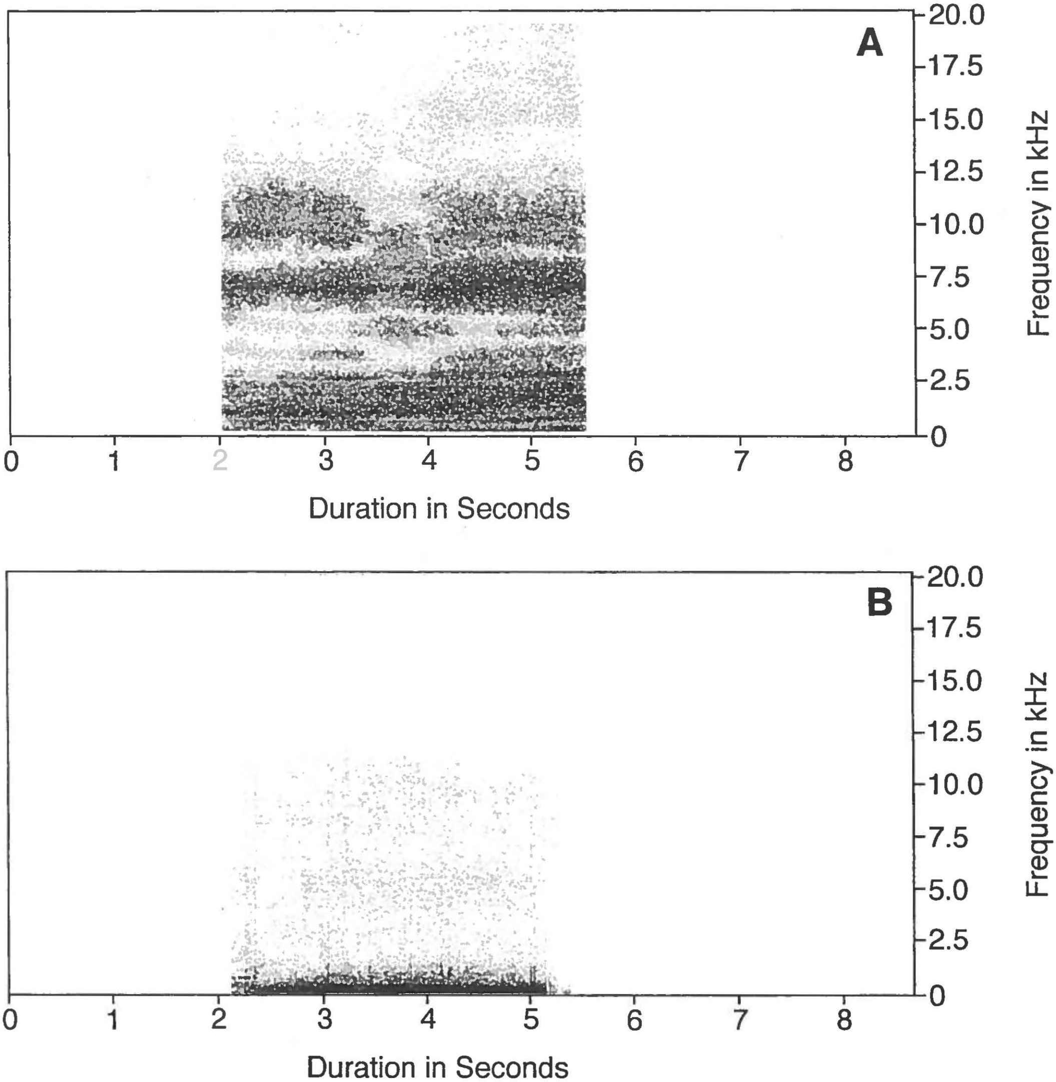

Fig. 3

Sonograms of defensive sounds produced by snakes. In these monograms the frequency of the sound is given on the Y-axis in kHz, the duration on the X-axis, and the intensity or amplitude of the sound is indicated by relative darkness, with the higher amplitude sounds being darker.

A: sonogram of a 3.7 second defensive hiss of Russell's viper (Daboia russelli).
Note that the sound spans from approximately 1.5 - 13 kHz with the dominant ('most intense) sound around 7.5 kHz.

B: sonogram of a 3.2 second "growl" produced by the king cobra (Ophiophagus hannah).
Note that most of the sound is composed of frequencies below 1.5 kHz.

■ BEHAVIORAL SIGNIFICANCE OF SOUND TO SNAKES

The acoustic biology of snakes is most problematic, and interesting, in relation to the behavioral significance of sound. For the sake of brevity, this discussion will be restricted to three subjects; prey location, defensive behavior, and intraspecific communication. Hearing is often listed as one of the senses used by snakes to located prey; the example most frequently given is of a rattlesnake stretching his head out to rest his chin on a log or path, thereby presumably increasing his auditory sensitivity to vibrations (Klauber, 1956). While this may in fact be true, there is scant experimental evidence to support this interpretation, or even to document that snakes use auditory information when foraging. Assuming that auditory cues are used for foraging, the dietary range of snakes makes it clear that this would not be a universal attribute of snakes - *Dasypeltis,* the African egg-eating snake, is unlikely to locate bird eggs by sound!

In terms of defensive behavior sound may play two roles: sounds made by the predator may alert the snake to the predator's presence, and snakes may produce sound as a means of warning or intimidating the predator. Anyone who has field collected snakes knows that they typically flee at the sound of heavy footsteps, but once again there is little experimental evidence for a behavioral response to groundborne vibration in snakes. Assuming such a response exists, it seems likely that it would vary with habitat. This may be where the differences between the somatic and auditory systems for hearing come into play.

There are several interesting questions about the warning or intimidation function of the sounds produced by snakes. Many snake species do not produce any warning sounds, some produce sounds only in response to particular predators, and - as anyone who has kept a large number of snakes knows - there is considerable intraspecific variation in the tendency to produce sound. How do the various sounds produced by snakes relate to predator avoidance? The growl of a king cobra is of lower frequencies than the hiss produced by most snakes; Russell's viper produces a very loud hiss (around 90 dB spl, equal to a noisy factory) while the cloacal pop of a Sonoran coral snake is very quiet (around 46 dB spl, which is less noise than a quiet restaurant). Do these differences in the acoustic properties of the sounds produced by snakes reflect strictly the different mechanisms used by the snakes, or have different species evolved different sounds in order to optimize their interactions with particular predators? Unfortunately, while we are learning more about the defensive sounds produced by snakes, we know very little about the impact these sounds have on the behavior of the predator. Not all of the sounds produced by snakes are true defensive behaviors; recent work (Kinney et al., 1998) has shown that the hiss of a rattlesnake is not a defensive behavior but a byproduct of rapid body inflation. At the present time it is not clear how common such incidental noises may be.

To date there is no evidence of intraspecific acoustic communication in snakes, that is to say, snakes making specific noises to influence the behavior of members of their own species (see Frankenberg and Wemer, 1992; Young 1997a). This is quite unusual and means that snakes are the largest group of terrestrial vertebrates which lack intraspecific acoustic communication. Historically this absence of intraspecific acoustic communication has been explained away on the presumption that snakes are deaf, but as described above this is incorrect. Furthermore, many snakes produce sounds with frequencies which fall within the experimentally determined range of auditory sensitivity in snakes. While some snake sounds may be too quiet to trigger a physiological response from the ear of another snake, many snakes produce sounds at intensities which exceed the experimentally determined threshold for hearing in snakes. Since the inner ears of at least some snakes can respond to the sounds snakes produce, why is there no evidence of acoustic communication in snakes?

It would appear that there are at least three possible explanations:

1. there may be some (as yet undocumented) cases of intraspecific acoustic communication in snakes;
2. the information content of the sounds 1.produced by snakes may preclude their use for intraspecific acoustic communication; and
3. snakes may simply not perceive the type of sounds which they produce.

Since all the snake sounds described to date lack ternporal pattering, frequency modulation, or amplitude modulation, they all have a very restricted capacity to transmit information - imagine if humans could only make an "uh" sound. While this low information content may be suitable for the clear warning message sent to a predator, it is probably too simple to serve as a mating call or some other form of intraspecific communication.The explanation based on perception is similar in that it postulates a fundamental deficiency in the snake. When discussing acoustic communication in Komodo dragons, Walter Auffenberg (1981) noted that these monitors are capable of responding to a variety of sounds including hisses, but that they generally show no interest in the hisses of other monitors - in essence, they ignore or fail to perceive intraspecific acoustic sounds.A sirmilar condition may exist in snakes in which the inner ear is physiologically capable of responding to the sounds made by snakes, yet this sound is simply not recognized by the auditory centers of the brain as important. Presumably, studies of the neural basis of hearing in snakes and the information content of snake sounds may increase our understanding of why this one group of vertebrates fails to communicate with one another using sound.

■ IN CONCLUSION

These three aspects of the acoustic biology of snakes (hearing, sound production and the behavioral significance of sound) make it clear that we are far from understanding the role sound plays in the biology of snakes. If we are to understand the evolution of snakes, and their interactions with the physical and biological world, we need to explore these basic aspects of the ophidian world.

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